Demography and Population Trend of Grizzly Bears in the Swan Mountains, Montana

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Abstract: *From 1987 to 1996 we used capture and telemetry methods to study the demography, movements, and population trend of grizzly bears* (Ursus arctos horribilis) *in wilderness and nonwilderness portions of the Swan Mountains of Montana. Most data were collected in the nonwilderness portion, which included public multiple-use lands and rural areas on and near private lands. Population density in nonwilderness averaged 1.6 bears/100 km^2. The annual total mortality rate (13.4%) was higher than that found in expanding brown bear* (Ursus arctos) *populations. A tenuous finite rate of increase (λ) of 0.977 (95% CI = 0.875–1.046) was related to high female mortality. Annual mortality rates for bears utilizing the rural and wilderness zones was 21 and 15 times higher, respectively, than for bears using only multiple-use lands. Our mortality, movement, and occupancy data suggest that the multiple-use zone is a population source area, and that wilderness and rural zones are sink areas. Mortalities in the wilderness zone were from mistaken identification during the black bear* (Ursus americanus) *hunting season and human defense of life. In the rural zone, mortalities were from malicious killing and the management removal of habituated or food-conditioned bears. We recommend that wildlife managers develop a conservation strategy to promote bear population stability or growth by improving female survival while minimizing bear conflicts on private lands. This would be accomplished by protecting core areas on public lands of superior habitat through access management, conducting a mandatory bear identification course for black bear hunters, and reducing anthropogenic foods on private lands. We also recommend a continuing population and habitat monitoring program.*

Demografia y Tendencias del Oso Grizzly en las Montañas Swan, Montana

Resumen: *De 1987 a 1996 utilizamos métodos de captura y telemetría para estudiar la demografa, movimientos y tendencias de los osos grizzly* (Ursus arctos horribilis) *en porciones silvestres y no-silvestres de las monatñas Swan, Montana. La mayoría de los datos fueron colectados en la porción no-silvestre, la cual incluye tierras públicas de usos múltiples y áreas rurales en o cerca de propiedades privadas. La densidad poblacional en áreas no-silvestres promedió 1.6 osos/100 km^2. La tasa de mortalidad anual (13.4%) fue más alta que la encontrada en poblaciones de osos pardos* (Ursus arctos) *en expansión. Una tenue tasa finita de crecimiento (λ) de 0.977 (95% CI = 0.875–1.046) estuvo relacionada con la alta mortalidad de hembras. Las tasas de mortalidad de osos que utilizan áreas rurales y zonas silvestres fue 21 y 15 veces más alta respectivamente, que la de osos que usan sólo tierras de usos multiples. Nuestros datos de mortalidad, movimiento y ocupación sugieren que la zona de usos múltiples es un área fuenta, mientras que las áreas silvestre y rural son áreas sumidero. Mortalidades en las zonas silvetres fueron ocasionadas por identificación errónea durante la temporada de caza del oso negro* (Ursus americanus) *y en defensa de vidas humanas. En la zona rural las mortalidades fueron por asesinatos maliciosos y remoción por manejo de osos habituados o condicionados a comida. Recommendamos a los manejadores de vida silvestre desarrollar una estrategia de conservación para promover la estabilidad o crecimiento de las poblaciones de osos improvisando la supervivencia de hembras al mismo tiempo que se minimizan los conflictos por osos en tierras privadas. Esto podría ser llevado a cabo protegiendo áreas medulares en las tierras públicas de hábitat superior mediante el manejo del acceso, conduciendo un curso de identificación para cazadores de osos negros y reduciendo alimentos de origen antropogénico en tierras privadas. También se recomienda un programa de monitoreo de la población y el hábitat.*

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Introduction

Management of natural resources at landscape or ecosystem scales is an important element of conservation. Unfortunately, few studies mounted at large scales help managers understand and address the ecological needs of wildlife in wider frameworks. Large-scale and long-term investigations of wide-ranging species such as the grizzly bear which document demography and movement are especially germane to the issue of ecosystem management.

Little information exists on the demography and population trend of grizzly bears in the northern Continental Divide ecosystem (NCDE), which were listed as a threatened species under the Endangered Species Act in 1975. There has been no effort to collect population data for the entire NCDE because of its large size ($\approx$22,000 km^2) and limited access (>50% roadless). Rather, past research has focused on localized areas within the NCDE in which collection of demographic data was secondary to other objectives (Servheen 1981; K. A. Aune and W. F. Kasworm, unpublished data).

Between 1987 and 1996, the Montana Department of Fish, Wildlife and Parks studied grizzly bears in the Swan Mountains. This area, composed of designated wilderness, multiple-use, and private lands, was a suitable location to investigate the effects of differing land-management philosophies and human-use patterns on the demography and trend of grizzly bears. We were particularly interested in determining the extent to which bears used these three jurisdictions; we evaluated mortality by jurisdiction to improve current knowledge of source-sink dynamics at a landscape scale.

Study Area

The study area is located in the western NCDE, approximately 24 km southwest of Glacier National Park. It has two primary divisions based on bear movements: designated wilderness lands and nonwilderness lands (Fig. 1). There are no roads or permanent human dwellings in the wilderness area, although an extensive trail system exists. Wilderness recreational activities include hiking, camping, hunting, and fishing.

Primary research emphasis was placed on a 1457-km^2, nonwilderness portion of the study area in the Swan Mountain Range, where all bears were captured. This area is bounded on the east by Hungry Horse Reservoir and on the west by the edge of contiguous forest in the Flathead River and Swan River valleys (Fig. 1). Grizzly bears are not tolerated by humans beyond the western boundary, an agricultural and suburban area. The nonwilderness area was further divided into two zones. We designated a 1152-km^2 area termed the "multiple-use zone" and a 305-km^2 area termed the "rural zone."

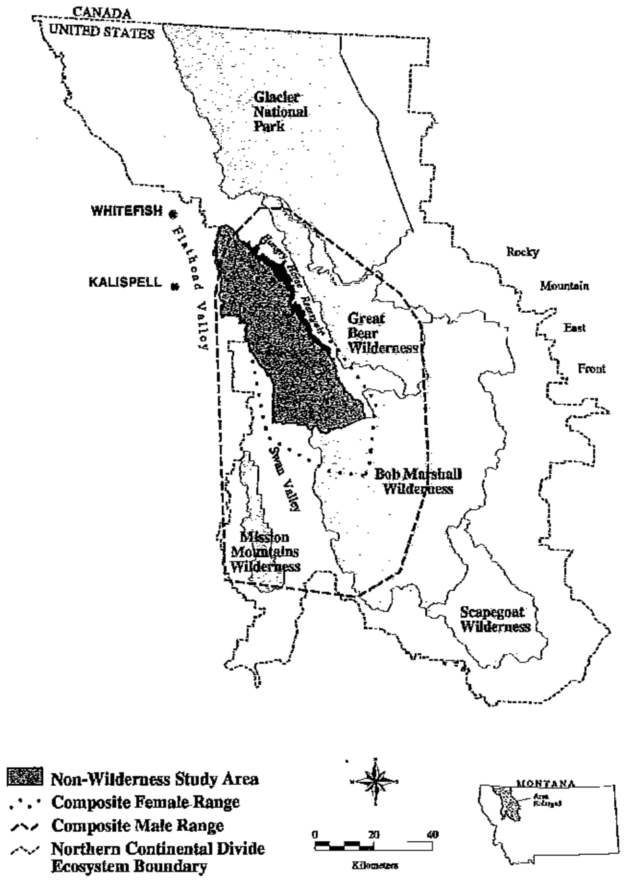

Figure 1. Study area in the Swan Mountains of western Montana showing nonwilderness and wilderness zones where grizzly bears were monitored. An area termed the rural zone was located in the Flathead and Swan valleys. Composite home-range polygons for male and female grizzly bears (1987–1995) relative to the NCDE are also shown.

The multiple-use zone is administered by the U.S. Forest Service and since the early 1950s has had a history of hydroelectric development, road building, and timber harvest. It contains 765 km of roads, of which 54% are legally open to vehicular traffic. The remaining roads are either permanently or seasonally closed to public traffic (Mace et al. 1996). Approximately 15% of the multiple-use zone has a history of timber harvest. The zone is used by the public for recreation, including a black bear hunting season.

The rural zone is adjacent to the multiple-use zone and is composed of private lands and adjacent roaded areas. Most private lands are roaded and developed for permanent homes, farms, or service facilities.

Human occupation in the Flathead Valley ranges from more than 39 humans/km^2 in the city of Kalispell to less than 10 humans/km^2 in the rural zone (1990 U.S. Census data). Human density in the Swan Valley is approximately 0.4 humans/km^2. In 1995 the greater Kalispell area had 42,814 residents (Kalispell Bypass Feasibility Study, Boyer Consulting Services).

The study area, under Pacific maritime climate, is characterized by heavily forested, rugged mountain topography; elevations varied from 914 to 2736 m. Over 50% of the area is coniferous forest intermixed with rock or shrub lands, avalanche chutes, and timber harvest units.

Methods

Capture and Telemetry

Grizzly bears were captured and radio-collared in nonwilderness lands primarily during spring from 1987 through 1996 (Mace et al. 1994). We designed capture sessions to mark as many bears as possible by modifying snaring methods and placement (Flowers 1977; White et al. 1982; Mace et al. 1994). We divided bears into six classes based on cementum annuli techniques (Stoneberg & Jonkel 1966): adult (≥5 years old) males and females, subadult (2–4 years old) males and females, cubs (0.5 years old), and yearlings (1.5 years old). To ensure that collars would not be worn permanently, we used cotton spacers to close the collar belting (Hellgren et al. 1988). Capture rate was defined as snare-nights per capture. A convex polygon was constructed from snare locations each year, from which the density of snares used each year (snares/100 km^2) was calculated. Grizzly bear locations were determined from fixed-wing aircraft 1–3 times each week as weather permitted throughout each bear's active season.

Dispersal

We defined dispersal as the period between family breakup and sexual maturity. The dates of family breakup and subsequent subadult movements were determined from aerial telemetry when either mother and offspring or both were radio-collared. We used the last visual observation of the family seen together or the date when the mother was first seen without her offspring. We could not verify the mother of subadults in all cases. In these instances we used weight of evidence—the location of bear at capture and the reproductive status of other resident marked and unmarked females—to link a subadult with the probable mother. Early movement patterns relative to the natal home range were estimated by calculating the percentage of locations of subadults within natal ranges. Natal ranges were defined as the 100% minimum convex polygon of the mother during the years prior to dispersal (Mohr 1947).

Mortality

Our most complete mortality records were from 1988 though 1996. Mortalities occurred in one of three zones, wilderness, multiple-use, or rural, and were categorized as human-caused or natural and "reported" or "unreported."

Categories of human-caused mortalities included those bears harvested legally, harvested as a result of being mistaken for black bears during a legal black bear hunting season, killed in defense of human life, removed because of habituated or food-conditioned behavior (Herrero 1985), killed maliciously, and killed by research activities. A killing was considered malicious when bears were shot and left when it was not black bear hunting season. Mortalities were classified as known or suspected. Suspected mortalities were those in which no carcass was located but extenuating circumstances suggested that a mortality had occurred (e.g., a collar with the belting cut). Possible mortalities or emigrations of marked male bears that had shed their radio collars were also considered suspect. These bears were frequently observed during snaring and photographic sighting sessions (Mace et al. 1994) for several years and then not seen again.

We assessed natural mortality using several criteria, including the lack of evidence suggesting human intervention, season, and location. Natural cub mortality was assumed when cubs disappeared between observation flights in remote locations. Natural mortality was also assumed if yearlings disappeared during spring (Hovey & McLellan 1996). Unreported mortalities included natural and human-caused mortalities that would not have been known had the bear not been radio-collared.

Annual cause-specific mortality rates and 95% confidence intervals (CI) were estimated for radio-collared bears by means of censored telemetry data with the computer program MICROMORT (Heisey & Fuller 1985). Annual rates were estimated in two ways. First, we estimated rates for the pooled sample of grizzly bears regardless of study area zone. Second, we estimated survival rates separately for four classes of bears: those living in only the multiple-use zone, those occurring in the multiple-use and rural zones, those living in the multiple-use and wilderness zones, and those using all three zones.

Population Size and Structure

We estimated local population size, density, and structure for the nonwilderness zone from radio-collared grizzly bears between 1989 and 1995 when most bears were instrumented. We were not able to calculate density estimates for the wilderness zone because no effort was made to capture bears there. Using the method of McLellan (1989*a*), we counted radio-collared bears and attendant young in proportion to the amount of time they spent in the nonwilderness zone each year. For example, an individual that never left the area counted as 1.0 bear, whereas an individual with only half its locations in the area counted as 0.5 bears. Percent time was then summed for all radio-collared individuals.

We estimated the number of unmarked bears in the nonwilderness zone by means of photographic sightings (Mace et al. 1994) and visual observations. Duplication of unmarked bears was reduced by examining physical characteristics, family group size, time, and location. Density estimates were calculated separately for the multiple-use and rural zones.

Using 100% minimum convex polygons, we constructed annual home ranges for all radio-collared bears (Mohr 1947) and calculated the percentage of the multiple-use zone occupied by grizzly bear home ranges.

Population Trend and Vital Rates

Finite rate of increase (λ) was calculated for the period 1987–1996 with a revised Lotka equation (Eberhardt et al. 1994; Hovey & McLellan 1996), which used survival and reproductive data obtained from radio-collared bears. For females we used four parameters: adult, subadult, yearling, and cub survival rates; age at first parturition; reproductive rate; and maximum age of reproduction.

We used the following equation (Hovey & McLellan 1996), which assumes a stable age distribution:

$$0 = \lambda^{a} - S_{a}\lambda^{a-1} - S_{c}S_{y}S_{s}^{a-2}\, m[1-(S_{a}/\lambda)^{w-a+1}], \quad (1)$$

where S_a, S_s, S_y, and S_c are adult, subadult, yearling, and cub survival rates, respectively. Annual survival rates, without a hazard function, were estimated with censored telemetry data obtained throughout each bear's active season (White & Garrott 1990). The survival rate of each female class except cubs was calculated as $\hat{S} = 1 -$ (recorded deaths/bear-years). Cub survival rates were estimated by $1 -$ (cub deaths/total number of cubs born).

The reproductive rate (m) per female was defined as the number of female cubs per interbirth interval. The number of cubs produced was ascertained from visual observations during spring, when families were still near the den. The interbirth interval was defined as the years of care given the litter plus any intervening period before the next birth (Hovey & McLellan 1996). We used only those females for which we had at least one complete interval. Demographic parameters were estimated by bootstrapping data 5000 times using the computer program BOOTER 1.0 (F. Hovey). Survival rate estimates derived from bootstrapping differed slightly from the cause-specific rates calculated using Heisey and Fuller's (1985) method. Age of first parturition (a) was fixed at 6 years and maximum age of female reproduction (w) at 25 years. The sex ratio of cubs was assumed to be 50:50. The average annual exponential rate of increase was calculated as $r = \log_e\lambda$ (Caughley 1977).

We used a λ cutoff point of 0.995 to describe local population trend. Values 0.995 or larger represented a stable to increasing population, those greater than 1.0 a growing population, and those less than 0.995 as population in decline.

Results

Capture

Fifty grizzly bears were captured 108 times (Table 1). Average capture rate was 80 snare-nights per capture. No new adult females were captured after 1990. Most adult males were also captured early in the study, but new subadults continued to be captured. Our sample of 50 grizzly bears was 58% female and 42% male. Median female and male ages at capture were 3 and 4 years, respectively (Fig. 2).

Local Population Size, Density, and Structure

Annual estimates of grizzly bear population size and age structure were determined for nonwilderness lands from 1989 through 1995, when a larger portion of the population had been marked and collared. On average, there were 22.6 marked grizzly bears present each year (Table 2). Solitary adult females and subadults constituted a greater proportion of the population than adult males. On average, 27.2% of the population was cubs or yearlings. Between 1989 and 1995, the annual density of marked bears averaged 1.6 ± 0.11 (SE) bears/100 km^2. We documented 2–14 additional unmarked bears each year (Table 2). Therefore, density estimates for nonwilderness lands were minimum values.

Annual density estimates were, on average, five times higher in the multiple-use zone ($\bar{x}$ = 1.76 bears/100 km^2) than the rural zone ($\bar{x}$ = 0.34 bears/100 km^2). The additional unmarked bears, all detected in the multiple-use zone, suggested an even more pronounced difference in bear density between zones.

Reproduction

Between 1989 and 1996 we documented 28 births from 17 litters of radio-collared females. Mean litter size was 1.64 ± 0.12 (SE) cubs/litter. Litter sizes were two cubs (65%) and one cub (35%). There were 4.0 ± 1.21 (SE) cubs born per year. Of the nine litters for which cub gender was known, the ratio averaged 64% female to 36% male. We observed no difference in litter size among four age classes (Craighead et al. 1995) of adult females ($\chi^2 = 2.19$, 6 df, $p = 0.90$).

Age of first reproduction was known for three females (ages 4, 5, and 8 years). Three other females had short and pinkish colored mammae when captured 1 year prior to cub production, suggesting that they could be included. Pooling all bears resulted in a mean age of first

Table 1. Grizzly bear capture effort and success from 1987 to 1996, Swan Mountains, Montana.

	Year										
Characteristic	*87*	*88*	*89*	*90*	*91*	*92*	*93*	*94*	*95*	*96*	*Total*
Capture polygon size (km^2)	101	866	866	518	560	999	559	425	37	30	
Snares	14	61	60	44	42	44	32	23	4	8	
Snare-nights	142	2196	2100	1296	750	789	814	402	40	98	8627
Snares/100 km^2	14	7	7	8	8	4	6	5	11	27	
Grizzly captures	6	25	19	15	12	7	16	5	2	1	108
Individuals	4	15	15	12	8	6	13	5	2	1	
Snare-nights/capture[a]	24	88	111	86	63	113	51	80	20	98	
New individuals[b]	4	13	5	8	5	3	6	4	1	1	50
New adult females	2	4	1	3	0	0	0	0	0	0	10
New adult males	0	6	1	0	0	0	1	0	0	0	8
New subadult females	2	2	2	1	3	3	3	2	1	0	19
New subadult males	0	1	1	4	2	0	2	2	0	1	13

[a] *Snare-nights per number of individuals.*
[b] *New individuals are defined as those grizzly bears not previously captured.*

reproduction of 6 years. Six complete interbirth intervals averaging 3 years (range 2–4 years) were documented for five females. We were unable to document the end of reproductive activity in older female grizzly bears. The older females successfully produced litters at age 20, 22, and 23 years. The reproductive rate was estimated to be 0.389 ± 0.104 (SE).

Mortality

We documented 35 grizzly bear mortalities (Table 3), 25 of which were grizzly bears wearing functional radio collars, 6 marked but without radio collars, and 4 bears unmarked. Of these mortalities 32 (91%) were known; we suspected 3 additional deaths. The average annual mortality each year from 1988 to 1996, counting all 35 cases, was 3.8 ± 0.97 (SE) bears (range = 0–10). We could not determine the cause of death in 5 of 35 cases involving marked and unmarked bears. Of the 30 known causes, most (67%) were human-caused. Natural death was the most common single category (Table 3). Of human-caused mortalities, 63%, 26%, and 11% occurred in the rural, the wilderness, and the multiple-use zone, respectively.

Most grizzly bears died during autumn (Table 3). Natural mortality was prominent during spring and summer, whereas management removal was the primary cause of loss during autumn. Two families (a female with two cubs and a female with two 2-year-olds) were removed from the study area after they became habituated and food-conditioned.

Annual cause-specific mortality rates from the pooled sample of bears (n = 25 marked and attendant young) were estimated from 170 bear-years of censored telemetry data (Table 4). Adult female mortality rates were highest for natural and unknown causes. Two adult females died of natural causes; a 15-year-old female

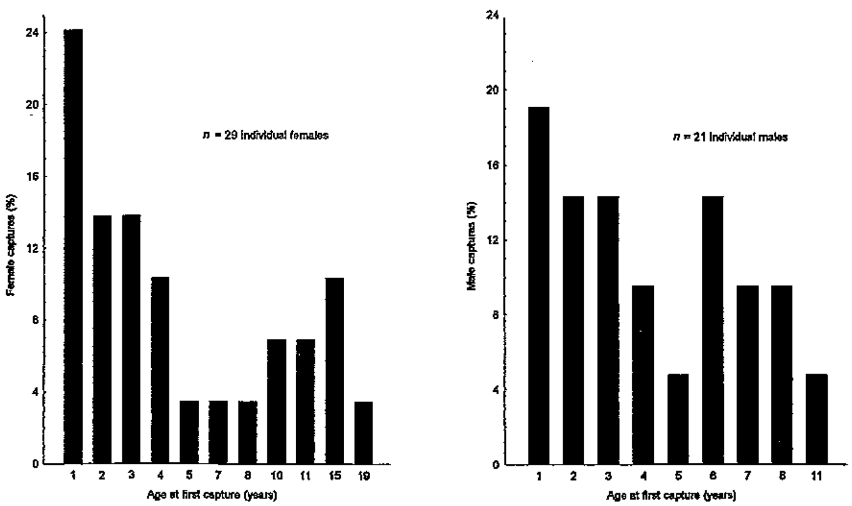

Figure 2. Age structure of 50 grizzly bears captured in the Swan Mountains, Montana between 1988 and 1995.

Table 2. Annual density estimates based on percentage of time radio-collared bears spent in the 1457-km^2 nonwilderness portion of the study area, 1989–1995, Swan Mountains, Montana.

	Radio-collared bears per class											*Unmarked bears*	
Year	*Cub*	*Yearling*	*Subadult male*	*Subadult female*	*Total subadult*	*Adult male*	*Adult female*	*Family group*[a]	*Solitary bears*	*Marked total*	*Marked density*[b]	*Solitary*	*Young*
89	4.0	0	1.4	4.5	5.9	4.2	5.5	2.0	15.9	19.6	1.3	9	5
90	4.3	1.0	3.7	3.9	7.6	3.9	9.1	3.1	20.6	25.9	1.8	3	2
91	10.0	3.1	1.9	2.0	4.9[c]	2.9	9.3	7.54	17.1	30.2	2.1	2	0
92	0	6.0	1.8	3.5	5.5	1.7	7.3	4.0	14.5	20.5	1.4	5	3
93	0	0	1.7	5.1	6.8	3.9	8.0	2.0	18.7	18.7	1.3	4	0
94	3.8	0	3.3	4.0	6.3	3.9	6.7	3.8	16.9	20.7	1.4	4	2
95	4.8	2.0	2.0	4.0	6.0	3.8	6.3	6.3	16.1	22.8	1.6	4	4
Mean	3.8	2.4	2.1	3.9	6.2	3.5	7.4	4.10	17.1	22.6	1.6		
Percentage	16.9	10.5	9.4	17.2	27.2	15.3	32.9		75.5				

[a] *The number of family groups is a subset of adult female class. For example, in 1989 there were 5.5 adult females, 2.0 of which had young.*
[b] *Bears/100 km^2.*
[c] *Includes one 2-year-old of unknown gender from marked female.*

was believed killed and fed upon by an adult male; a female, accompanied by two cubs, probably died in an avalanche.

Mortality due to mistaken identification during black bear hunting seasons was the leading cause of subadult female mortality (Table 4). One subadult female (age 2) died during the spring breeding season of natural wounds believed inflicted by a radio-collared adult male. Cubs were most susceptible to natural mortalities.

Adult males were most likely to die during ungulate hunting season in defense-of-life by hunters in the wilderness zone after the bears confiscated harvested elk (*Cervus elaphus*). One adult male was killed on private land while breaking into a dog kennel for dog food. Subadult males were equally susceptible to malicious killing and mistaken identification.

The annual mortality rate for all classes and causes was 13.62% (95% CI = 8.52–18.44%). The annual human-caused mortality rate for all classes was 7.33% (95% CI = 3.42–11.09%). The annual unreported mortality rate was 8.70% (95% CI = 4.70%–12.90%).

Grizzly bears spent varying amounts of time in the wilderness, multiple-use, and rural zones (Table 5). The 17.6% annual mortality rate for bears utilizing multiple-use and rural zones was 21 times higher than the rate for those living only in the multiple-use zone. The 12.9% annual mortality rate for grizzly bears living in both the multiple-use and wilderness zones was 15 times higher

Table 3. Cause- and class-specific mortality records for 35 grizzly bears, 1988–1996, Swan Mountains, Montana, of which the season of death was known for 32 deaths.[a]

	Cause of mortality								
	Natural	*Mistaken identity*	*Legal hunt*	*Self-defense*	*Management removal*	*Malicious*	*Research*	*Unknown*	*Total (%)*
Class									
Adult									
M	1	0	0	3	0	0	0	2[b]	6 (17.1)
F	2	2	0–1[c]	0	1–1[c]	0	0	2	9 (25.7)
Subadult									
M	0	0	0	0	0	2	0	1[b]	3 (8.6)
F	1	3	0	0	0	0–1	0	0	5 (14.3)
Cub	6	0	0	0	0	0	0	0	6 (17.1)
Yearling[d]	0	1	0	0	2–2[c]	0	1	0	6 (17.1)
Total (%)	10 (28.5)	6 (17.1)	1 (2.8)	3 (8.6)	6 (17.1)	3 (8.6)	1 (2.8)	5 (14.3)	35 (100)
Season									
Spring	5 (15.6)	3 (9.3)	0	1 (3)	0	1 (3.1)	1 (3.1)	2 (6.2)	13 (40.4)
Summer	4 (12.5)	0	0	0	0	0	0	0	4 (12.5)
Autumn	0	3 (9.3)	1 (3.1)	2 (6.2)	6 (18.7)	2 (6.2)	0	1 (3.1)	15 (46.6)

[a] *Numbers represent known and suspected mortality of marked and unmarked bears. Not all marked bears were radio-collared at time of death, nor did they all die within the study area.*
[b] *Suspected mortality of unknown cause.*
[c] *Where two numbers are presented, the first represents the number of marked bears and the second represents the number of unmarked bears.*
[d] *Yearlings include bears over 0.5 years old until year of dispersal.*

Table 4. Cause-specific annual mortality rates of radio-collared grizzly bear classes based on censored telemetry data, 1987–1996, Swan Mountains, Montana.

	Class					
Parameter	*Adult male*	*Adult female*	*Subadult male*	*Subadult female*	*Cub*	*Yearling*[a]
Sample Size[b]	13/29	16/56	11/11	15/21	28/23	25/30
Survival	0.873 (0.764–0.997)	0.899 (0.826–0.979)	0.828 (0.638–1.00)	0.828 (0.688–0.996)	0.77 (0.626–0.949)	0.90 (0.80–1.0)
Mortality cause						
Natural		0.034 (0–0.079)		0.043 (0–0.125)	0.23 (0.05–0.37)	
Mistaken identification		0.017 (0–0.050)	0.086 (0–0.247)	0.129 (0–0.265)		
Self-defense	0.095 (0–0.197)[c]					
Management		0.017 (0–0.050)				0.063 (0–0.148)
Malicious			0.086 (0–0.247)			
Research						0.032 (0–0.092)
Unknown	0.032 (0–0.093)	0.034 (0–0.079)				
Mortality category						
Human-caused	0.095 (0–0.197)	0.033 (0–0.080)	0.171 (0–0.387)	0.129 (0–0.265)		0.095 (0–0.191)
Unreported	0.032 (0–0.093)	0.067 (0–0.131)	0.171 (0–0.387)	0.129 (0–0.265)	0.23 (0.05–0.37)	

[a] *Yearlings include bears over 0.5 years old until year of dispersal.*
[b] *Number of bears per radio-years.*
[c] *Annual mortality rate estimate (lower-upper 95% CI).*

than for those bears utilizing only the multiple-use zone, and all mortalities occurred in the wilderness zone.

Movements, Occupancy, and Dispersal

Male grizzly bears moved through a large portion of the NCDE (Fig. 1). The 100% MCP for all males during the study (7852 km^2) was 4.3 times that of the pooled sample of females (1843 km^2). During the entire study, no radio-collared females crossed the Hungry Horse Reservoir on the eastern side of the study area (Mace & Waller 1997) or the highly urbanized and roaded Flathead Valley. Further, we observed no movement north into Glacier National Park across urbanized areas. Movement into wilderness areas was observed for males and those female grizzly bears with home ranges along this boundary. The large composite minimum convex polygon range for males was due partially to several males captured on the southern periphery of the study area. Although these males spent most of their time elsewhere, they returned to the study area each spring during the breeding season.

Annual MCPs were used to estimate occupancy of the multiple-use zone each year. The occupancy averaged 73% and varied from 39% (13 radio-collared bears) to 82% when 18 bears were radio-collared. These occupancy measures were minimal because additional unmarked bears were present.

Table 5. Annual mortality rates for four classes of grizzly bears based on the amount of time spent in multiple-use, rural, and wilderness lands, Swan Mountains, Montana.

	Mean time in zone combination (%)					
Class of bear	*Multiple-use*	*Rural*	*Wilderness*	*Bear-years*	*Mortalities*[a]	*Annual mortality rate (95% CI)*
Multiple-use	100	0	0	116.3	1	0.009 (0.0–0.025)
Multiple-use/rural	77	24	0	41.4	8[b]	0.176 (0.058–0.280)
Multiple-use/wilderness	48	0	52	21.6	3[c]	0.129 (0–0.260)
Multiple-use/rural/wilderness	76	10	14	11.2	0	0

[a] *Human-induced mortalities are for subadult and adult bears independent of their mother.*
[b] *All mortalities occurred in rural zone.*
[c] *All mortalities occurred in wilderness area.*

Date of family breakup was estimated for 16 young grizzly bears (n = 11 female, 4 male, and 1 unknown). All young grizzly bears dispersed during spring (median = 24 May, n = 16; range = 7 May–28 June). We knew the age at breakup of 18 subadults; 14 (78%) dispersed as 2-year-olds and the remainder dispersed as 3-year-olds.

Most movement pattern data were obtained for only the first 2 years subsequent to family breakup because collars were designed to fall off young bears and because some bears died. We were able to evaluate dispersal movement patterns of 12 radio-collared grizzly bears (n = 9 female, 3 male) relative to their natal home range. The average percentages of telemetry locations within natal ranges for dispersing females during years 0 (year of breakup) and 1 were 75% and 78%, respectively. Percentages for males during years 0 and 1 were 33% and 9%, respectively.

Two of three subadult males for which we had movement data had obtained human food after moving into the rural zone. One of these bears died, and we suspect that the other died as well. The third subadult male was not food-conditioned to our knowledge but was killed illegally after moving into the rural zone.

Population Trend

Our estimated finite rate of increase (λ) was 0.977 (95% CI = 0.875–1.046), given the fixed and estimated demographic variables (Table 6). The uncertainty in λ, as indicated by the proportion of the variance explained, was due primarily to variation in subadult female survival (56.07%) and secondarily to adult female survival (37.25%). Cub and yearling survival explained a small proportion of the variance (Table 6).

The probability that the population was declining was 69%, stable to increasing 31%, and increasing 27% (Fig. 3). The annual exponential rate of increase (r) was 0.02 (−0.13–0.045), indicating that it would take about 30 years to observe a population halving, given the long-term stability of vital rates.

Discussion

We believe that the local population dynamics of grizzly bears in the Swan Mountains is an example of source-sink demography. Areas or subpopulations for which fecundity exceeds mortality are termed *sources*, and demographically inviable areas or subpopulations are termed *sinks* (Pulliam 1988; Donovan et al. 1995). We encapsulated evidence suggesting that the multiple-use zone was near capacity for grizzly bears given current landscape structure and function, and that the rural and wilderness zones were sink areas. But we were unable to conduct formal analyses of source-sink dynamics (e.g., Doak 1995) because we could not partition all vital rates or estimate trend by wilderness and nonwilderness zones.

Twenty-eight cubs were born to radio-collared grizzly bears, and we documented 25 deaths of radio-collared bears and attendant young. Estimate of trend supported these birth and death statistics, indicating stability or exceedingly slow population decline. Annual density estimates also suggested that the population was relatively stable, and therefore that the lower and upper bounds of the 95% confidence intervals for λ were not observed. The uncertainty in our estimate of trend was due primarily to high subadult female mortality. Because of small sample sizes, age of first reproduction and reproductive longevity were fixed variables; their contribution to the observed trend could not be inferred. In other studies, however, these parameters had little affect on estimates of trend (Eberhardt et al. 1994; Hovey & McLellan 1996).

The mean annual density estimate for the nonwilderness area (1.6 bears/100 km^2) was greater than the 0.15–1.3 bears/100 km^2 for the eastern portion of the NCDE

Table 6. Estimated annual survival rates by class, reproductive rate, and population trend of grizzly bears, 1987–1996, Swan Mountains, Montana.

	Estimates of survival and rate of change					
Parameter	*Sample size*	*Estimate*[a]	*Lower 95% CI*	*Upper 95% CI*	*SE of estimate*	*Variance proportion (%)*[b]
Adult female survival (S_a)	16/56[c]	0.899	0.785	0.966	0.046	37.25
Subadult female survival (S_s)	15/21[c]	0.825	0.629	0.962	0.089	56.07
Yearling survival (S_y)	25/30[c]	0.906	0.906	1.000	0.049	1.53
Cub survival (S_c)	28	0.785	0.643	0.928	0.076	2.87
Age first parturition (a)	fixed	6.0				
Reproductive rate (m)[d]	6	0.261	0.214	0.316	0.026	2.88
Maximum age (w)	fixed	25.0				
Lambda (λ)	5000	0.977	0.875	1.046	0.043	

[a] *Survival rate estimates may differ from those in Table 4, as described in Methods.*
[b] *The proportion of variance in lambda explained by each parameter.*
[c] *Number bears per bear-years.*
[d] *Reproductive rate is for female cubs only. Assumed sex ratio at birth is 50:50.*

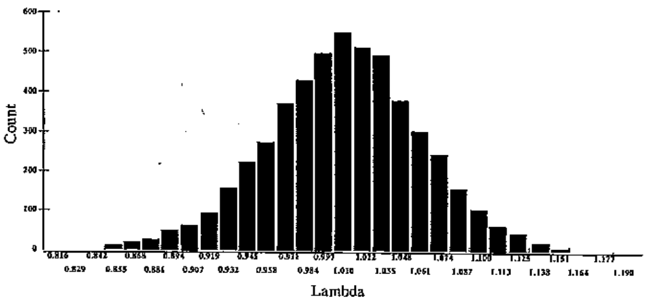

Figure 3. Distribution of 5000 bootstrap simulations on the value of lambda for grizzly bear population of Swan Mountains, Montana.

(K. A. Aune & W. F. Kasworm, unpublished data) and the 1.2 bears/100 km^2 for the greater Yellowstone ecosystem (Eberhardt & Knight 1996). Our density estimates exceeded most other published estimates from Canada and the Northwest Territories (Pearson 1975; Russell et al. 1979; Interagency Grizzly Bear Committee 1987; Clarkson & Liepins 1994; Wielgus & Bunnell 1994; Wielgus et al. 1994), and were similar to those reported for interior Alaska where salmon runs are absent (Miller et al. 1997).

We further demonstrated that the annual density of grizzly bears in the multiple-use zone was five times greater than in the rural zone. Source-sink models generally assume that, when $\lambda > 1$, net movement will be out of the source habitat (Doak 1995). If sink habitats are attractive to bears, however, they may attract individuals in a density-independent fashion. We believe that the rural zone was attractive because of the availability of spring and autumn forage, ungulate carcasses on winter ranges, and anthropogenic foods (e.g., domestic fruit orchards and garbage).

High percent occupancy of the multiple-use zone, low fecundity, high mortality, high density, and stable trend all suggest that the carrying capacity may have been closely met, given the current distribution of natural resources and levels of habitat degradation and human use.

Density dependence theory predicts that vital rates will be suppressed as population density increases. Unexploited brown bear populations may stabilize in a density-dependent fashion, although the form is unclear and possibly derived from multiple causes (Harris 1984). At higher densities all reproductive parameters may be suppressed, or in some cases only mortality rates may increase (Bunnell & Tait 1980). Litter size in the Swan Mountains was among the lowest reported in the literature (Interagency Grizzly Bear Committee 1987). Interbirth intervals may also be affected in a density-dependent fashion: intervals may increase at higher population densities. The role of adult males in population regulation is unclear, but high densities of adult males may affect vital rates (McCullough 1981; Young & Ruff 1982; Stringham 1983). At high densities, adult males may either kill, exile, or compete with females for resources. If sustained over time, a high mortality rate for adult males in the Swan Mountains may cause an influx of immigrant males, which could suppress rates further. We have no evidence of males killing cubs. We could not determine the cause of death for four of six cubs because they simply disappeared between telemetry flights. We believe, however, that two adult males did kill other grizzly bears. In one case a 10-year-old male, possibly an immigrant, was implicated in the death of a 2-year-old female. In a second case, we believe that a resident 11-year-old male killed and ate a 15-year-old female.

Quantitative estimates of grizzly bear population trend are available for few areas in North America. A local population in southern British Columbia, Canada (adjacent to the NCDE) (McLellan 1989*a*, 1989*b*, 1989*c*; Hovey & McLellan 1996) increased ($\lambda = 1.085$), given an annual female survival rate of 0.94 and a density of six bears/100 km^2. A recent derivation of λ (1.046) for grizzly bears in Yellowstone National Park (Eberhardt et al. 1994) was obtained from uncensored telemetry data and survival rates for subadult and adult female grizzly bears of 0.89 and 0.92. Wielgus et al. (1994) showed no population growth with subadult and adult female survival rates of 0.78 and 0.96. Unfortunately, no estimate of λ was provided by K. A. Aune and W. F. Kasworm (unpublished data) for the only other intensively studied portion of the NCDE. They reported maximum annual survival rates for adult females, subadult females, and cubs/yearlings of 0.967, 0.918, and 0.852, respectively. These higher survival rates, coupled with a larger estimated litter size and shorter interbirth interval (2.6 years), suggest that the local population in this area was stable or increasing.

The annual mortality rate for grizzly bears in the Swan Mountains was higher than that for other brown bear populations in North America (Craighead et al. 1974; Sidorowicz & Gilbert 1981; Harris 1984; McLellan 1989*b*, Eberhardt et al. 1994; K. A. Aune & W. F. Kasworm, unpublished data). Bunnell and Tait (1980) recommended that total annual mortality not exceed 12.5%, which was lower than the 13.62% observed here. Generally, annual survival rates for females must equal or surpass 90% to support population growth (Eberhardt 1990), as indicated by the positive trends for Yellowstone National Park (Eberhardt et al. 1994) and southern British Columbia (Hovey & McLellan 1996). Our study population was probably at the maximum sustainable mortality, beyond which a decline would be certain.

Habitat managers will be challenged to increase bear numbers and improve long-term local population trend in source-sink landscapes such as the Swan Mountains. The projected human growth for the Flathead Valley area was estimated to be 17% by the year 2000, so managers must develop strategies to improve grizzly bear survival and habitat security concurrent with an increasing number of humans using and living in grizzly bear habitat. Managers should be aware that even small incremental levels of habitat degradation can lead to declines in precariously stable populations (Doak 1995) such as that of the Swan Mountains.

Conclusions and Recommendations

Effective management for the Swan Mountain grizzly bear population must include several key elements: (1) establishing a population goal, (2) understanding the value of public and private lands to grizzly bears, and (3) identifying opportunities to improve management.

Population Goal

Conservation is one of three population management objectives and is most appropriate for small or declining populations (Caughley 1977; Miller 1990). We recommend a conservation strategy for grizzly bears in the Swan Mountains because (1) the trend for the entire NCDE population is unknown; (2) our estimates of local population size, trend, and other vital rates were not without error, and there was a nontrivial probability of population decline; (3) mortality rates for adult and subadult females were higher than those of other locals and may represent the maximum beyond which a decline in the local population would be certain; and (4) the local population was semi-isolated because of human development, including hydroelectric development.

The purpose of a conservation goal for grizzly bears in the Swan Mountains is to realize more confidently population stability or growth. The challenge will be to manage for more grizzly bears by improving survival rates while minimizing use of private lands by bears. We believe that an increase of 5–10 adult females could be achieved before other factors—primarily space—would become limiting.

Value of Public and Private Lands

Most grizzly bears spent the majority of their time on public multiple-use lands, suggesting that they provided necessary life requisites. Some grizzly bears used privately owned valley habitats, sometimes outside of the NCDE recovery area, for several reasons: (1) an abrupt topographical transition exists between mountain and valley habitats (Fig. 1); (2) the valley is snow-free longer than much of the mountain habitat, so vegetal foods sought by grizzly bears are available longer in this area; (3) high densities of white-tailed deer (*Odocoileus virginianus*) winter in the valley, and their carcasses are a food source during spring; and (4) for bears so inclined, a multitude of anthropogenic foods is available.

We believe that space, more so than food resources, is limiting to grizzly bears in the area and is the factor most crucial to use of the rural zone. The Swan Mountains are only 19 km wide between Hungry Horse Reservoir and the valley; grizzly bears appear to be confined between these two features. At present home-range overlap for females averages 24% (Mace & Waller 1997), and about 73% of the space is occupied. If space is truly limiting, efforts to orient bears away from private lands by increasing the vegetal food base (e.g., burning or planting fruit-bearing shrubs) on public lands (Craighead et al. 1995) will have little mitigative value.

Specific Recommendations

We offer the following recommendations to achieve the goal of increasing female survival rates while reducing conflicts in the rural zone.

PROVIDE HABITAT SECURITY BY PROTECTING CORE AREAS

Management emphasis in the NCDE is placed on protection of female grizzly bears (Dood et al. 1986; U.S. Fish and Wildlife Service 1993), and therefore areas required by females to survive should receive high priority for habitat conservation. Because most mortalities occur in the rural zone, further human access restrictions on federal lands will not significantly reduce grizzly bear deaths in landscapes such as those studied here. Until private lands are sanitized, however, federal lands should be considered invaluable source areas and managed to reduce mortality. This could be accomplished by establishing high-security core areas that include seasonal habitats (Mace et al. 1996). The negative effects of human access to grizzly bears via roads are well understood (Archibald et al. 1987; Mattson et al. 1987; McLellan & Shackleton 1988; Kasworm & Manley 1990; Mace et al. 1996). Therefore, access management should be a strategy within core areas to minimize disturbance and illegal mortality.

Limiting female mortality will have the greatest conservation benefit for this population. The two biggest sources of human-caused mortality were management removal and mistaken identification during the spring black bear season. We strongly urge that a mandatory education program be implemented to ensure that resident and nonresident black bear hunters can differentiate grizzly bears from black bears.

REDUCE CONFLICTS ON PRIVATE LANDS

Private lands and areas of concentrated human use on public lands are attractive to grizzly bears because of the presence of human or livestock foods, bird feeders, domestic fruits, and garbage. Efforts to minimize food conditioning and habituation through county planning efforts, improved garbage disposal, and increased education and enforcement will be necessary to reduce bear mortality. Managers should seek legal means to discourage unsanitary conditions on public and private lands.

MONITOR MORTALITY AND HABITAT EFFECTIVENESS

Without a monitoring program, managers will find it difficult to choose the correct management strategy for grizzly bears in the Swan Mountains (Miller 1990). Human-caused mortality is the leading cause of the observed trend in the Swan Mountains, and in this context mortality is an exceedingly important parameter to measure, especially for females. We recommend a monitoring program for a radio-collared sample of about five adult and subadult female grizzly bears to estimate female survival and reproductive rates. Observed deviations from the rates reported here would serve as an index to population trend.

Assessment of female grizzly bear mortality should be accompanied by an ongoing program that measures changes in habitat effectiveness on private and public lands. We suggest that a habitat monitoring program be conducted at two scales: (1) a large, landscape scale through methods such as those described in Mace et al. (1997) and (2) a finer scale for private lands through cooperation with county planning offices and the public, because even small, incremental losses of habitat can result in population decline (Doak 1995). This program would monitor inconspicuous changes in land-use practices that would not be evident at landscape scales.

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